

Evaluation of the Functional Response of Selected Arthropod Predators on Bollworm Eggs in the Laboratory and Effect of Temperature on Their Predation Efficiency

M. N. PARAJULEE,^{1,2} R. B. SHRESTHA,¹ J. F. LESER,³ D. B. WESTER,⁴ AND C. A. BLANCO⁵

Environ. Entomol. 35(2): 379–386 (2006)

ABSTRACT A functional response study of the eight most common arthropod predators of cotton bollworm, *Helicoverpa zea* (Boddie), eggs was conducted in the laboratory. Predators were starved for 24 h, and single predators were exposed to different prey density treatments. Predation response was observed at 6, 12, and 24 h after feeding trials began. At the highest prey density (150 eggs per predator), *Hippodamia convergens* Guerin-Meneville and *Collops quadrimaculatus* (F.) adults and *Chrysopa oculata* Say larvae showed the highest consumption rates (116, 85, and 119 eggs/24 h, respectively), followed by *H. convergens* larvae (51 eggs/24 h), adult *Geocoris punctipes* (Say) (45 eggs/24 h), and adult *Scymnus loewii* Mulsant, *Orius insidiosus* (Say), *Notoxus* spp., and *Nabis capsiformis* Germar (1, 1, 10, and 12 eggs/24 h, respectively). Adult *Notoxus* spp., *N. capsiformis*, and *O. insidiosus* showed type 1 functional response, whereas adult *C. quadrimaculatus*, *G. punctipes*, *H. convergens*, and larval *H. convergens* and *C. oculata* showed type 2 response. All predators consumed the highest number of bollworm eggs at 35°C and the lowest numbers at 15°C; predation rate at 35°C was four times higher than that at 15°C. The prey density-dependent behavior of predators and effect of temperature on their predation behavior are discussed.

KEY WORDS functional response, attack rate, predation, cotton bollworm eggs, biological control

THE COTTON BOLLWORM, *Helicoverpa zea* (Boddie), is a key pest of cotton in Texas and throughout the cotton belt (Parajulee et al. 1998, 2004, Williams 2004). Several studies have shown the potential of naturally occurring predator species in suppressing bollworm eggs and larval infestations in cotton (Ewing and Ivy 1943, Lingren et al. 1968, Ridgway and Lingren 1972, Bryson and Schuster 1975, McDaniel and Sterling 1979, Arnold 1999). However, the information on functional response and comparative ability of bollworm predator species to consume the target pest is lacking. This information is critical to implementation of natural enemy conservation and augmentation of natural biological control. The information on laboratory functional response could be used to infer the basic mechanism of the predator-prey interactions in the field (Houck and Strauss 1985). The number of prey that an individual predator kills is a function of prey density and is known as functional response (Holling 1966). Effectiveness of a predator is directly related to the type of their functional response.

Arthropod predators display one of three typical functional responses, but the response may vary with crop phenology, habitat heterogeneity, age of predator, and other biotic and abiotic factors. In a type 1 functional response, the number of prey killed increases linearly at a constant rate up to a maximum and remains constant as prey density further increases (combination of density-dependent and density-independent responses). The response is estimated by a linear equation

$$N_e = \alpha + \beta N \quad [1]$$

where N_e = number of prey eaten, N = prey density (number of prey offered), and α and β = the intercept and slope of the prediction line, respectively.

In a type 2 functional response, the number of prey killed approaches asymptote hyperbolically as prey density increases (declining proportion of prey killed or inverse density dependence). This type of response is estimated most commonly by a curvilinear function (Holling 1966),

$$N_e = \frac{a N T}{1 + a N T_h} \quad [2]$$

where N_e = number of prey eaten, a = the attack constant or instantaneous search rate, N = initial prey density, T = total available time, and T_h = handling time (or the time taken by the predator to search, capture, consume, and digest one prey). In this model,

¹ Texas Agricultural Experiment Station, 1102 E FM 1294, Lubbock, TX 79403.

² Corresponding author, e-mail: m-parajulee@tamu.edu.

³ Texas Cooperative Extension, 1102 E FM 1294, Lubbock, TX 79403.

⁴ Texas Tech University, Department of Range, Wildlife, and Fisheries, Box 2125, Lubbock, TX 79409.

⁵ USDA-ARS SIMRU, Stoneville, MS 38776.

Table 1. Total bollworm egg consumption in 24 h and the consumption rate (no. consumed per hour) of several arthropod predators in a no-choice laboratory feeding trial

Predator species	Prey density	Total eggs eaten in 24 h	Consumption rate (eggs/h)
Red-cross beetle (<i>Collops quadrimaculatus</i>)	150	85.1 ± 10.29	3.5 ± 0.43b
Insidious flower bug (<i>Orius insidiosus</i>)	30	1.2 ± 0.25	0.1 ± 0.01d
Big-eyed bug (<i>Geocoris punctipes</i>)	100	44.7 ± 5.48	1.9 ± 0.23c
Convergent lady beetle (<i>Hippodamia convergens</i>)			
Adult	150	116.0 ± 10.66	4.8 ± 0.44a
Larva	150	51.2 ± 16.85	2.1 ± 0.70c
Green lacewing (<i>Chrysopa oculata</i>)	150	119.3 ± 29.11	5.0 ± 1.21a
Hooded beetle (<i>Notoxus</i> spp.)	40	10.2 ± 2.18	0.4 ± 0.09d
Pale damsel bug (<i>Nabis capsiformis</i>)	30	11.8 ± 4.51	0.5 ± 0.19d
Scymnus beetle (<i>Scymnus loewii</i>)	30	1.0 ± 0.77	0.04 ± 0.03d
Leafhopper assassin bug (<i>Zelus renardii</i>) ^a	30	0	0
Crab spider (<i>Misumenops</i> spp.) ^a	30	0	0

Numbers followed by the same letter were not significantly different ($\alpha = 0.05$, LSD).

^a No eggs were consumed during the 24-h exposure.

prey density remains constant, and the handling time limits the number of prey eaten within a fixed time period. However, because the experiment is usually conducted without prey replacement, the prey density declines as the experiment proceeds. Roger's random predator equation (Rogers 1972, Juliano 1993) is generally used to overcome the prey replacement problem in Holling's model as follows:

$$N_e = N \{1 - \exp[a(T_h N_e - T)]\}, \quad [3]$$

where N_e = number of prey eaten and N = initial prey density.

The type 3 functional response occurs when the number of prey killed approaches asymptote as a sigmoid function (increase in proportion of prey killed up to inflection point and then decrease in proportion). This is the density-dependent response. Type 3 functional response can be derived using Hassell's model (Hassell 1978) where the attack rate (a) is a hyperbolic function of the prey density as follows:

$$a = \frac{d + hN}{1 + cN} \quad [4]$$

and by substituting the value of a to the Holling's equation, we get the type 3 model as:

$$N_e = \frac{dNT + hN^2 T}{1 + cN + dNT_h + bN^2 T_h} \quad [5]$$

where N_e = number of prey eaten, T = total time, T_h = handling time, and b , c , and d are constants. After using the integral of random predator equation (Rogers 1972), the type 3 functional response can be estimated as

$$N_e = N \{1 - \exp[(d + bN)(T_h N_e - T) / (1 + cN)]\}, \quad [6]$$

where parameters were as described above.

Generally the average bollworm egg density in the field is less than one egg per cotton leaf because moths rarely lay large numbers of eggs on the same leaf, although four to five eggs on a single leaf is not un-

common under a heavy bollworm infestation or late in the season. In general, it is not feasible to evaluate the functional response of a predator in such a low egg density either in the field or in a laboratory. Nevertheless, it is important to understand the consumption behavior of the predators when presented with a greater prey density. The laboratory study of functional responses to artificially high prey densities gives an indication of the potential of the predator to suppress the pest under conditions of high pest pressure in the field. Objectives of this study were to evaluate the bollworm egg consumption efficiency of common predators, to determine their functional response to varied prey densities under laboratory conditions, and to quantify the effect of temperature on their predation efficiency.

Materials and Methods

This study was conducted in the Cotton Entomology Laboratory at the Texas Agricultural Experimental Station, Lubbock, TX. The functional responses of 10 commonly occurring arthropod predators [convergent lady beetle, *Hippodamia convergens* Guerin-Meneville, green lacewing, *Chrysopa oculata* Say, red-cross beetle, *Collops quadrimaculatus* (F.), big-eyed bug, *Geocoris punctipes* (Say), Scymnus lady beetle, *Scymnus loewii* Mulsant, insidious flower bug, *Orius insidiosus* (Say), hooded beetle, *Notoxus* spp., pale damsel bug, *Nabis capsiformis* Germar, leafhopper assassin bug, *Zelus renardii* (Kolenati), and crab spiders, *Misumenops* spp.] were evaluated (Table 1). All predators were collected from several cotton fields using a sweep net or beat bucket. Predators of mixed sex but uniform size and vigor were sorted from the field-collected samples and held without food and water for 24 h. The second and third instars of convergent lady beetle and green lacewing larvae were used for the study, whereas the adult stage was evaluated for all predators, except for the green lacewing. Bollworm eggs were used as model prey and were obtained from the USDA-ARS, SIMRU, Stoneville, MS.

Table 2. Arthropod predator species and prey (bollworm eggs) density treatments used in the laboratory functional response study

Predator species	Prey density treatments
Red-cross beetle	5, 10, 25, 50, 75, 100, 150
Insidious flower bug	1, 2, 4, 6, 8, 10, 20, 30
Big-eyed bug	5, 10, 25, 50, 75, 100
Convergent lady beetle adult	10, 25, 50, 75, 100, 150
Convergent lady beetle larva	5, 10, 25, 50, 75, 100, 150
Green lacewing	10, 25, 50, 75
Hooded beetle	5, 10, 20, 40
Pale damsel bug	5, 10, 15, 20, 30
Scymnus beetle	5, 10, 15, 30
Leafhopper assassin bug ^a	NA
Crab spider ^a	NA

^a No functional response was conducted because of no feeding response (see Table 1).

NA, not applicable.

Cotton Bollworm Egg Consumption Rate. Because research information was unavailable on the bollworm egg consumption rate of most of the selected predator species at different prey densities and under laboratory conditions with the exception for *H. convergens*, *G. punctipes*, *O. insidiosus*, and *Z. renardii* (Ewing and Ivy 1943), a preliminary feeding test was conducted to examine if the predator would use bollworm eggs as prey and to determine the maximum consumption rate per 24 h. Predators were starved for 24 h, and 100 bollworm eggs were offered per predator, replicated five times. The treatment arena consisted of bollworm eggs arranged singly in rows and glued with tap water on a fresh cotton leaf in a plastic petri dish (100 by 15 mm). The eggs were arranged in rows to facilitate counting. Frequent observations were made to ensure that bollworm egg density of 100 per predator was sufficient for 24-h consumption. Predators that consumed at least one egg were considered a potential predator and the total number of eggs eaten by each successful predator in 24 h was recorded.

After the preliminary experiment, eight species were identified as potential bollworm egg predators (Table 1). These were collected from the field and starved for 24 h before initiating the study, conducted at $29 \pm 2^\circ\text{C}$ and 12:12 (L:D) h. Ten individuals from each predator species or stage were confined separately and provided with prey eggs ad libitum (Table 1). The numbers of eggs eaten per predator were recorded 24 h after feeding began. Prey consumption rate (number eaten per hour) for each predator was calculated, and data were analyzed using analysis of variance (ANOVA; PROC GLM; SAS Institute 2002) with predator species as a source of variability.

Functional Response Study. The functional response study was conducted with the eight most common predator species selected from the preliminary feeding test (Table 1). Response was measured by randomly assigning different densities of bollworm eggs (1–150 eggs per density treatment) to each predator species in a petri dish. Density treatments ranged from five to eight depending on predator species (Table 2). Each treatment was replicated 5–10 times. The maximum and minimum prey densities for each pred-

ator were determined based on a preliminary feeding study as described previously. The treatment arena consisted of bollworm eggs arranged singly in rows and glued with tap water on a fresh cotton leaf in a plastic petri dish (100 by 15 mm). The eggs were arranged in rows to facilitate counting. The experiment was conducted at 29°C and a photoperiod of 12:12 (L:D) h. Moist cotton swabs and filter papers (9 cm) were used to keep the bollworm eggs and cotton leaf moist during the experiment. Predators confined with fixed numbers of egg densities were kept undisturbed until the response was measured. The prey consumption was recorded at 6, 12, and 24 h after the predator was released to the experimental arena. The 12-h data were used to analyze the functional response of most of the predators. Because convergent lady beetles consumed all eggs at lower densities in 12 h, the 6-h data were used to derive the functional response parameters. The 24-h data were used for slower feeding insidious flower bugs, Scymnus beetles, hooded beetles, and pale damsel bugs.

The polynomial logistic regression of proportion of prey consumed versus initial prey density was performed using a categorical data modeling program (CATMOD; SAS Institute 2002) to determine the type of functional response (Juliano 1993). If the linear parameter calculated by logistic regression was not significantly different from zero, there was no influence of increased prey density on the proportion of prey consumption and the type 1 functional response (equation 1) was fitted to that data. If the linear parameter was significant and negative, a negative relationship between the increased prey density and prey consumption rate occurred, and the type 2 functional response (equation 3) was selected for those data. If the linear parameter was significant and positive, increased prey density would result in positive predation response, and the type 3 functional response (equation 6) model was chosen for that data set.

Because the experiment was conducted without prey replacement, the integral of random predator equation (Rogers 1972, Juliano 1993) model was used to estimate the parameters for both type 2 and type 3 functional responses. The functional response models were fitted by the maximum likelihood method in the nonlinear regression procedure (NLIN; SAS Institute 2002). The functional response parameters, search rate (a) and handling time (T_h), were calculated for each predator.

Effect of Temperature on Prey Consumption Rate. Five predator species were evaluated for their functional response as affected by temperature. Temperature treatments included 15, 20, 25, 30, and 35°C maintained in growth chambers with 12:12 (L:D) h photoperiod. The predators included red-cross beetles, big-eyed bugs, convergent lady beetles (adult and larva separately), insidious flower bugs, and green lacewing larvae. For each temperature treatment and predator species or stage, a single predator was confined in a petri dish with prey eggs provided ad libitum and replicated 10 times. The number of prey consumed per predator was recorded at 12, 24, 36, and 48 h

Table 3. Selection of functional response model based on analysis of maximum likelihood estimates of parameters (\pm SE) using proportion prey eaten as a polynomial function of prey density

Predator	Linear	Quadratic	Cubic	Best-fit model
Hooded beetle	-0.7962 ± 0.3644	0.0430 ± 0.0204	-0.00064 ± 0.000309	Type 1
Pale damsel bug	1.0255 ± 0.6513	-0.0468 ± 0.0358	0.000687 ± 0.000610	Type 1
Insidious flower bug	-0.1088 ± 0.1467	0.00721 ± 0.0103	-0.00020 ± 0.000206	Type 1
Scymnus beetle	-2.3618 ± 2.1800	0.2105 ± 0.1810	-0.00536 ± 0.00454	Type 1
Red-cross beetle	-0.1285 ± 0.0248^a	0.00103 ± 0.000301^a	$-2.84\text{E}^{-6} \pm 1.092\text{E}^{-6}^a$	Type 2
Convergent lady beetle adult	-0.0296 ± 0.0145^a	0.000255 ± 0.000198	$-1.07\text{E}^{-6} \pm 7.732\text{E}^{-7}$	Type 2
Convergent lady beetle larva	-0.0834 ± 0.0224^a	0.000781 ± 0.000303^a	$-2.46\text{E}^{-6} \pm 1.17\text{E}^{-6}$	Type 2
Green lacewing	-0.3457 ± 0.0977^a	0.00833 ± 0.00232^a	-0.00006 ± 0.000016^a	Type 2
Big-eyed bug	-0.1541 ± 0.0508^a	0.00174 ± 0.000857	$-7.55\text{E}^{-6} \pm 4.45\text{E}^{-6}$	Type 2

^a Significant at $P < 0.01$.

after predator introduction to the prey. Response data for each predator were analyzed using a repeated measures ANOVA (PROC GLM; SAS Institute 2002) with temperature and predation duration as sources of variability. Also, the rate of change in bollworm egg predation in relation to temperature was calculated for each predator using a linear regression analysis of number of eggs consumed per predator per 24 h as a function of temperature.

Results

Cotton Bollworm Egg Consumption Rate. Laboratory no-choice feeding trials showed that 10 of the 15 predatory arthropods commonly encountered in Texas High Plains cotton could serve as bollworm egg predators. The green lacewing larva and convergent lady beetle adult showed the highest consumption rates (119 and 116, eggs/24 h, respectively) followed by the adult red-cross beetle (85 eggs/24 h), convergent lady beetle larvae and big-eyed bugs (51 and 45 eggs/24 h, respectively), and pale damsel bug, hooded beetle, insidious flower bug, and Scymnus beetle (12, 10, 1, and 1 eggs/24 h, respectively; $df = 9,47$; $F = 21.9$; $P = <0.0001$; Table 1). The leafhopper assassin bug and crab spider did not consume bollworm eggs in our repeated laboratory evaluations.

Functional Response. The logistic polynomial regression analysis (Table 3) showed that the four slower feeding predators (pale damsel bug, hooded beetle, Scymnus beetle, and insidious flower bug) displayed the type 1 functional response (Tables 3 and 4; Fig. 1) as indicated by nonsignificant linear parameters. Those predators showing the type 1 response had no change in feeding behavior with the change in

prey population. Although the total number of prey consumed by the pale damsel bug ($R^2 = 0.93$), hooded beetle ($R^2 = 0.97$), Scymnus beetle ($R^2 = 0.90$), and insidious flower bug ($R^2 = 0.25$) increased linearly with increase in prey population, the rate of change in consumption rate was near constant (Table 4), except in case of insidious flower bug, which showed a weak relationship between predation rate and prey density. Convergent lady beetle larvae, green lacewing larvae, convergent lady beetle adults, red-cross beetles, and big-eyed bugs had a significant, negative linear parameter, indicating a type 2 functional response (Tables 3 and 5; Fig. 1). These predators consumed higher number of prey with higher prey availability, but the rate of consumption decreased with increasing prey density. None of the predators evaluated in this study displayed the type 3 functional response.

Effect of Temperature on Predation Rate. All five predators consumed significantly the highest numbers of bollworm eggs at 35°C and significantly the lowest numbers of bollworm eggs at 15°C (Fig. 2). Consumption rates of red-cross beetles were similar at 25 (91 ± 9.4 eggs), 30 (98 ± 9.2 eggs), and 35°C (105 ± 7.9 eggs) treatments. The predation rate of big-eyed bugs increased significantly at 25 and 30°C compared with that at 20°C, whereas the feeding rate at 35°C was significantly higher than at lower temperatures. Both convergent lady beetle adults and larvae had a fairly continuous increase in bollworm egg consumption rate as temperature increased from 15 to 35°C (Fig. 2). Consumption rates of green lacewing larva were lower at 20 (36 ± 6.3 eggs), 25 (31.3 ± 4.5 eggs), and 30°C (44.6 ± 7.5 eggs), but the rate increased significantly at 35°C (59.7 ± 6.4 eggs). The insidious flower bug consumed a lower number of eggs at all temperatures

Table 4. Estimated intercept and slope parameter coefficients of the type 1 functional response displayed by the four slow-feeding arthropod predators in the laboratory study^a

Predator species	Intercept (α)			Slope (β)			R^2
	Parameter	SE	$P > t $	Parameter	SE	$P > t $	
Pale damsel bug	-1.54	± 0.88	0.18	0.302	± 0.05	0.01	0.93
Insidious flower bug	0.765	± 0.43	0.13	0.045	± 0.03	0.20	0.25
Hooded beetle	0.257	± 0.73	0.76	0.246	± 0.03	0.01	0.97
Scymnus beetle	-1.00	± 0.56	0.21	0.172	± 0.04	0.05	0.90

^a Total time available for predation was 24 h for all predators.

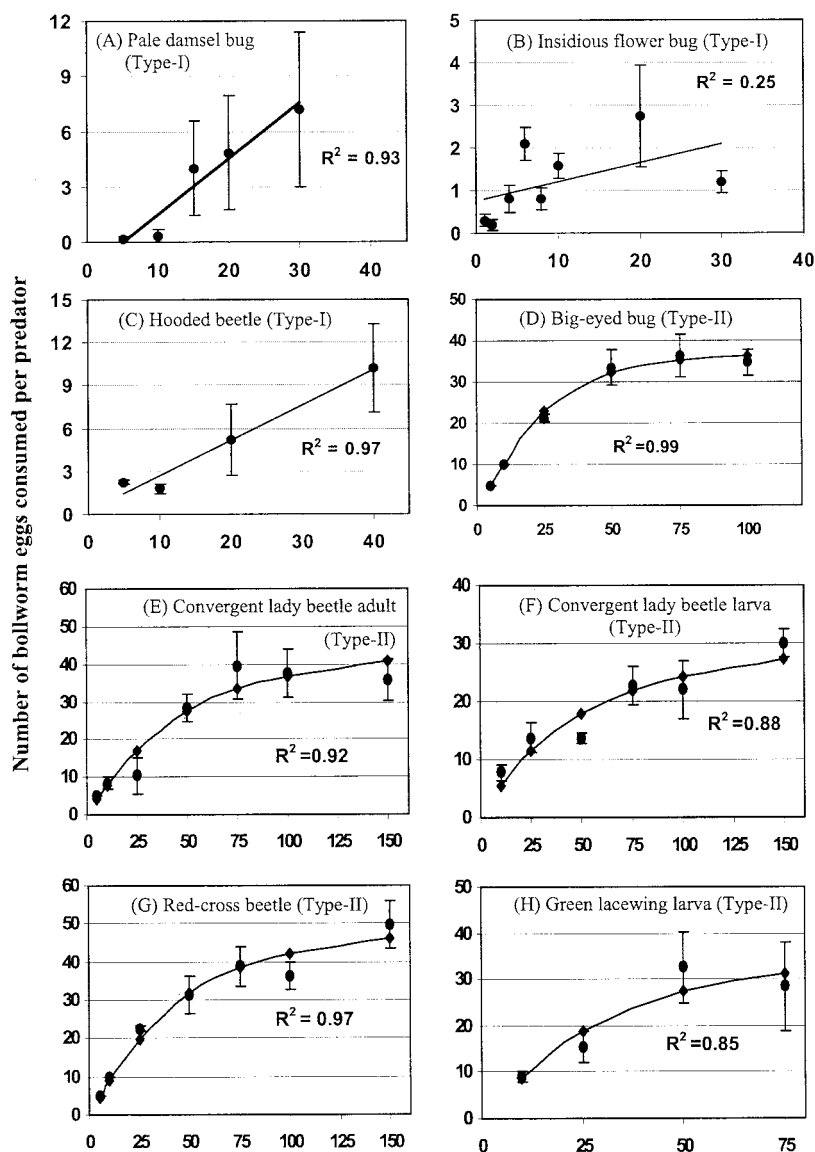


Fig. 1. Functional response of eight cotton arthropod predators to bollworm eggs. Closed circles (\pm SE) represent the averaged observed response, and the solid line represents the model prediction. Total time available for predation was 24 h for predators that displayed type I responses and 12 h for predators that displayed type II responses, except for convergent lady beetle adult (6 h).

compared with other predators tested. Consumption was lowest at temperatures from 15 to 25°C and significantly higher at 30 and 35°C. The increase in convergent lady beetle adult consumption rate from 15 to 35°C was 655% followed by big-eyed bug (444%), convergent lady beetle larva (383%), insidious flower bug (356%), green lacewing (336%), and red-cross beetle (244%). The convergent lady beetle adult (slope = 8.2) and larva (slope = 5.7) were most sensitive to change in temperature, followed by the red-cross beetle (slope = 3.5), big-eyed bug (slope = 3.4), green lacewing (slope = 0.6), and insidious flower bug (slope = 0.1; Table 6).

Discussion

This study indicated that Texas High Plains cotton agroecosystems support a diverse complex of cotton arthropod predators with a significant potential to suppress bollworm eggs. The green lacewing, convergent lady beetle, red-cross beetle, big-eyed bug, pale damsel bug, hooded beetle, insidious flower bug, and *Scymnus* beetle showed a considerable potential to serve as bollworm egg predators, in that order. A preliminary, exploratory work of Ewing and Ivy (1943) suggested that *Chrysopa rufilabris* (Burmeister) consumed the highest number of bollworm eggs

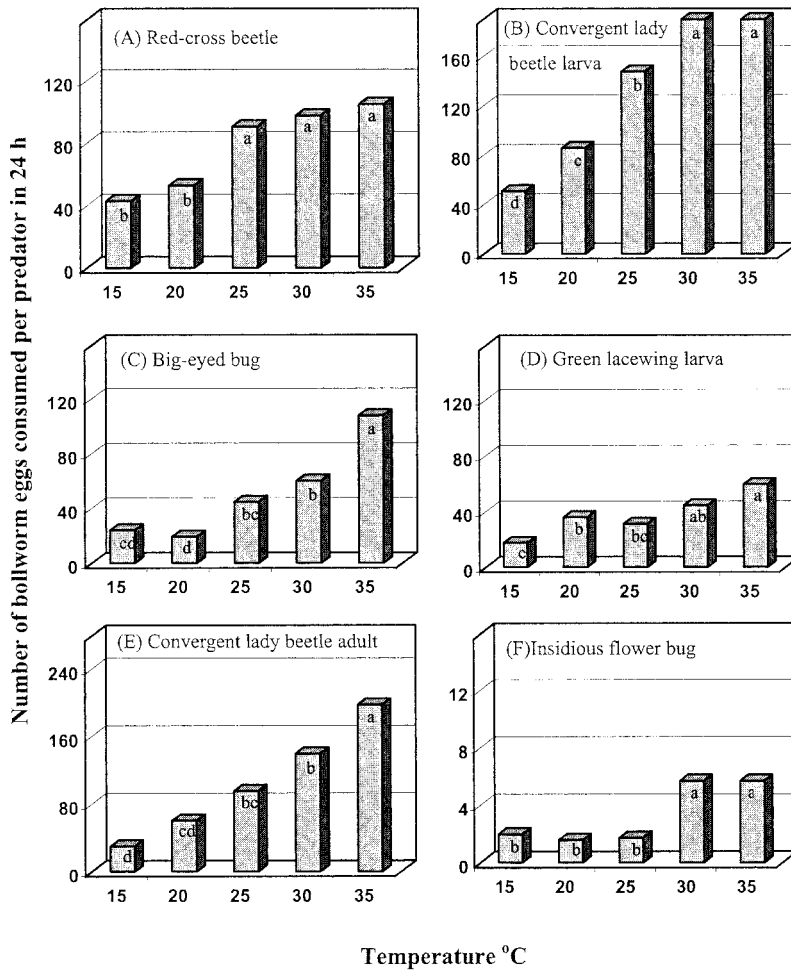


Fig. 2. Effect of temperature on bollworm egg consumption by different arthropod predators. Means followed by the same letter were not significantly different ($P > 0.05$).

(27.4 eggs/d), followed by *H. convergens* adults (24.5 eggs/d) and larvae (14.1 eggs/d), *Collops balteatus* (LeConte) (8.8 eggs/d), *G. punctipes* (2.7 eggs/d), *O. insidiosus* (2.3 eggs/d), and *Z. renardii* (1.8 eggs/d). These data suggest that the consumption rates of the predators evaluated in our study followed a similar

trend as suggested by Ewing and Ivy (1943). Although Ewing and Ivy (1943) reported a low level of bollworm egg consumption by *Z. renardii*, it did not consume bollworm eggs in our repeated laboratory evaluations. Crab spiders also did not consume bollworm eggs in

Table 5. Estimated handling time and attack rate for cotton arthropod predators that displayed type 2 responses in the laboratory study^a

Predator species	Attack rate (a)		Handling time (T_h)	
	Parameter	SE	Parameter	SE
Convergent lady beetle				
Adult	0.2917 ^b	±0.1427	0.1200 ^b	±0.0261
Larva	0.0759 ^b	±0.0304	0.3432 ^b	±0.0732
Green lacewing	0.2200	±0.2583	0.3053 ^b	±0.1403
Red-cross beetle	0.2074 ^b	±0.0766	0.2225 ^b	±0.0275
Big-eyed bug	0.4896	±0.3807	0.3049 ^b	±0.0362

^a Total time available for predation was 12 h for all predators, except for lady beetle adult (6 h).

^b Significant at 95% confidence interval.

Table 6. Rate of change in bollworm egg predation in relation to temperature by selected arthropod predators

Predator	Rate of change in predation (eggs ± SE/°C) ^a
Convergent lady beetle adult	8.20 ± 0.61a
Convergent lady beetle larva	5.68 ± 1.61ab
Red-cross beetle	3.54 ± 0.59b
Big-eyed bug	3.40 ± 0.87b
Green lacewing	0.59 ± 0.54c
Insidious flower bug	0.11 ± 0.07c

Numbers followed by the same letter were not significantly different ($\alpha = 0.05$, LSD).

^a Rate of change in predation = slope of the regression where no. of eggs consumed per 24 h = $f(\text{temp})$.

our study. This study clearly indicated that most predator species evaluated in this study consumed and showed potential to suppress bollworm eggs in the field, but a field predation study is still needed to quantify their actual pest suppression ability. Sansone and Smith (2001) reported that 70–95% bollworm mortality caused by predation could be expected in the egg and first-instar stages. Our study estimated that *O. insidiosus* consumed 1.2 bollworm eggs per day, which is similar to that reported by Lingren et al. (1968) and McDaniel and Sterling (1979), who estimated that *Orius* spp. consumed one bollworm egg per day. Predation, especially by the numerically dominant *Orius* spp., was suspected to be contributing to the disappearance of eggs and first-instar bollworm larvae in Brazos Valley cotton (McDaniel and Sterling 1979). Green lacewing larvae and convergent lady beetle adults were the most voracious predators of bollworm eggs in our study, with 119 and 116 eggs consumed per predator per day, respectively. Ewing and Ivy (1943) reported an average of 24.5 eggs consumed per convergent lady beetle per day, but a single predator consumed as many as 275 eggs in a 24-h period. Although the average consumption rate reported by Ewing and Ivy (1943) is much lower than we found in this study, it is clear that they also recognized that the convergent lady beetle and green lacewing larva were the most voracious predators of bollworm eggs. However, the feeding preference of these predators may change when alternate prey such as the cotton aphid, *Aphis gossypii* Glover, is available. Ewing and Ivy (1943) reported that convergent lady beetles consumed 13 bollworm eggs and 9 cotton aphids per predator per day when both prey were available ad libitum simultaneously.

The functional response study also indicated that the convergent lady beetle, green lacewing, and red-cross beetle were the most voracious predators of bollworm eggs. The increment in prey consumption rate was constant for the pale damsel bug, hooded beetle, and insidious flower bug. The prey mortality caused by predation by the convergent lady beetle, green lacewing, red-cross beetle, and big-eyed bug increased, but at a decreasing rate with an increase in prey density. A predator's functional response may vary with sex and developmental stages of the predator as well as that of prey, searching arena, and the abiotic environment (Parajulee et al. 1994, O'Neil 1997, Donnelly and Phillips 2001, Stewart et al. 2002, Allahyari et al. 2004). The actual field environment is much different than the laboratory setting because of the variation in factors such as temperature, wind, rain, surface area, prey type, and biotic complex, so that the functional response in the field or simulated field is expected to be different than that in the laboratory (Wiedenmann and O'Neil 1991, Parajulee et al. 1994). Also, the impact of a particular predator species on prey suppression depends on the predator-prey ratios and the intraguild predation (Rosenheim et al. 1995). Nevertheless, the information from laboratory functional response studies can be used to

narrow down the selection of effective predators for more detailed field studies.

Fluctuations in the environment, particularly the temperature, can influence the predation behavior of arthropod predators. Therefore, it is one of the important factors to be considered while estimating the prey suppression by different predators in natural biological control (Frazer and Gilbert 1976). Xia et al. (2003) reported a direct relationship between temperature and prey searching rate of a lady beetle where the search rate of *Coccinella septempunctata* L. increased significantly for each 5°C temperature increase from 15 to 35°C. A strong positive relationship between consumption rates and temperature for all predator species evaluated in this study suggests that cotton arthropod predators in general are more active and have higher predation potential during the mid and late summer period in the Texas High Plains when average daily temperatures are >30–35°C. However, simulated field studies should be conducted for better understanding of the mechanism of higher rates of predation in a fluctuating high temperature regimen.

Acknowledgments

The authors thank R. Strauss and S. Juliano for help with data analysis, S. Carroll, L. Jones, and M. Shrestha for help with the research, and M. Arnold for critical review of the manuscript. The U.S. EPA Region 6 and International Cotton Research Center (Lubbock, TX) provided partial funding for this research.

References Cited

- Allahyari, H., P. A. Fard, and J. Nozari. 2004. Effect of host on functional response of offspring in two populations of *Trissolcus grandis* on the sunn pest. *J. Appl. Entomol.* 128: 39–43.
- Arnold, M. D. 1999. Natural mortality of the bollworm in Texas High Plains cotton. MS thesis, Texas Tech University, Lubbock, TX.
- Bryson, C. T., and M. F. Schuster. 1975. Effectiveness of a spotted lady beetle as a predator of the bollworm on cotton. *J. Econ. Entomol.* 68: 273.
- Donnelly, B. E., and T. W. Phillips. 2001. Functional response of *Xylocoris flavipes* (Hemiptera: Anthracoridae): effect of prey species and habitat. *Environ. Entomol.* 30: 617–624.
- Ewing, K. P., and E. E. Ivy. 1943. Some factor influencing bollworm populations and damage. *J. Econ. Entomol.* 36: 602–606.
- Frazer, B. D., and N. Gilbert. 1976. Coccinellids and aphids: a quantitative study of the impact of adult ladybirds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). *J. Entomol. Soc. Br. Columbia.* 73: 33–56.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, NJ.
- Holling, C. S. 1966. Functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* 48: 1–87.
- Houck, M. A., and R. E. Strauss. 1985. The comparative study of functional responses: experimental design and statistical interpretation. *Can. Entomol.* 115: 617–629.

- Juliano, S. A. 1993. Nonlinear curve fitting: predation and functional response curves, pp. 159–182. In S. M. Scheiner and J. Gurevitch (eds.), *Design and analysis of ecological experiments*. Chapman & Hall, New York.
- Lingren, P. D., R. L. Ridgway, and S. L. Jones. 1968. Consumption by several common arthropod predators of eggs and larvae of two *Heliothis* species that attack cotton. *Ann. Entomol. Soc. Am.* 61: 613–618.
- McDaniel, S. G., and W. L. Sterling. 1979. Predator determination and efficiency on *Heliothis virescens* eggs in cotton using ^{32}P . *Environ. Entomol.* 8: 1083–1087.
- O'Neil, R. J. 1997. Functional response and search strategy of *Podisus maculiventris* (Heteroptera: Pentatomidae) attacking Colorado potato beetle (Coleoptera: Chrysomelidae). *Environ. Entomol.* 26: 1183–1190.
- Parajulee, M. N., T. W. Phillips, and D. B. Hogg. 1994. Functional response of *Lyctocoris campestris* (F.) adults: effects of predator sex, prey species, and experimental habitat. *Biol. Control.* 4: 80–87.
- Parajulee, M. N., D. R. Rummel, M. D. Arnold, and S. C. Carroll. 2004. Long-term seasonal abundance of *Helicoverpa zea* and *Heliothis virescens* (Lepidoptera: Noctuidae) moths in the Texas High Plains. *J. Econ. Entomol.* 97: 668–677.
- Parajulee, M. N., J. E. Slosser, and E. P. Boring, III. 1998. Seasonal activity of *Helicoverpa zea* and *Heliothis virescens* (Lepidoptera: Noctuidae) detected by pheromone traps in the Rolling Plains of Texas. *Environ. Entomol.* 27: 1203–1219.
- Ridgway, R. L., and P. D. Lingren. 1972. Predaceous and parasitic arthropods as regulators of *Heliothis* populations. *Southern Coop. Ser. Bull.* 169: 48–56.
- Rogers, D. 1972. Random search and insect population models. *J. Am. Ecol.* 41: 369–383.
- Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois, and B. A. Jaffee. 1995. Intraguild predation among biological control agents: theory and evidence. *Biol. Control.* 5: 303–335.
- Sansone, C. G., and J. W. Smith. 2001. Natural mortality of *Helicoverpa zea* (Lepidoptera: Noctuidae) in short-season cotton. *Environ. Entomol.* 30: 112–122.
- SAS Institute. 2002. *SAS/STAT user's guide*, SAS Institute, Cary, NC.
- Stewart, C. D., S. K. Braman, and A. F. Pendley. 2002. Functional response of the azalea plant bug (Heteroptera: Miridae) and green lacewing, *Chrysoperla rufilabris* (Neuroptera: Chrysopidae), two predators of the azalea lace bug (Heteroptera: Tingidae). *Environ. Entomol.* 31: 1184–1190.
- Wiedenmann, R. N., and R. J. O'Neil. 1991. Laboratory measurement of the functional response of *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae). *Environ. Entomol.* 20: 610–614.
- Williams, M. R. 2004. Cotton insect losses—2003. *Proceedings of the Beltwide Cotton Conference*, Nashville, TN, 5–9 January, 2003.
- Xia, J. Y., R. Rabbinge, and W. van der Werf. 2003. Multi-stage functional response in a lady beetle aphid system: scaling up from the laboratory to field. *Environ. Entomol.* 32: 151–162.

Received for publication 18 May 2005; accepted 3 August 2005.